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Introduction - Chapter 1

This report, “Diet Composition, Diet Overlap, and Size of 14 Species of Forage Fish Collected Monthly in Prince William Sound, Alaska, 1994-1996,” summarizes results from three years of Forage Fish Diet Overlap projects. Its purpose is to provide an overview of food habits and potential competition between forage species using combined project data. The species examined include juveniles from several Teleost families: the Salmonidae-- pink salmon (*Oncorhynchus gorbuscha*) chum salmon (*O. keta*), and sockeye salmon (*O. nerka*); the Osmeridae-- eulachon (*Thaleichthys pacificus*) and capelin (*Mallotus villosus*); Bathylagidae-- northern smoothtongue (*Leuroglossus schmidti*); the Gadidae-- pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*) and Pacific tomcod (*Microgadus proximus*); the Clupeidae-- Pacific herring (*Clupea pallasii*); the Ammodytidae-- Pacific sandlance (*Ammodytes hexapterus*); the Zaproridae-- prowlfish (*Zaprora silenus*); the Gasterosteidae-- threespine stickleback (*Gasterosteus aculeatus*); and the Trichodontidae-- Pacific sandfish (*Trichodon trichodon*). Each of these species is commonly encountered in the area and/or abundant at some time within the study period. The < 150 mm size range of forage fish means that some species (e.g., herring, pollock, salmon) are seabird prey as juveniles, then outgrow the classification, while others are considered to be forage species throughout their life history (e.g., capelin and sandlance). Some species may be more familiar than others, and some may not be thought of as traditional “forage fish” (Springer and Speckman, 1997). The salmonids, for example, are well-known, commercially important as adults, planktivorous, “small schooling species” during their early marine period of residency (Groot and Margolis, 1991), and can contribute large proportions to the diets of piscivorous seabirds (Scheel and Hough, 1997). They are also important because of their high densities during the period of spring outmigration when the habitats they transition are also utilized by “traditional” forage species for feeding. Prowlfish and sandfish are two of the little known forage species which are sometimes pelagic and sometimes cryptic because of their association with either jellyfish or sediments, respectively. Prowlfish can be frequent or infrequent dietary components of diving seabirds, but provided 25% of dietary biomass delivered to tufted puffin (*Lunda cirrhata*) chicks (Hatch and Sanger, 1992; Roseneau et al, 1998). Sandfish occurred in diets of nearshore diving birds, such as pigeon guillemots foraging on demersal or schooling species (Golet et al, 1998). Because differences in the quality of forage fish are sufficient to influence prey selection by seabirds (Roby et al, 1998), their trophic relationships with one another are important to consider in an ecosystem study. Summarizing by month allows diet comparisons by season between individual species or family groups and by year for a few species examined interannually in July.

The annual report of the 1994 Forage Fish Diet Overlap project (Willette et al., 1995) limited results principally to the August-September directed sampling collections, which included zooplankton and epibenthic prey samples and thus allowed an investigation of prey selection (Willette et al., 1995). Prey field samples that directly correspond to the catches from May-July, 1994, are not available. Nonetheless, a seasonal and interannual assessment of food habits, diet overlap and prey partitioning among forage fish is important. Trophic interactions between species cannot be understood without an understanding of which species are common and abundant and how often their distributions overlap in space and time. For example, the carrying capacity of PWS to support numerous planktivore species may reach its limits when densities of

fish are greatest, such as when strong year classes of herring or capelin appear or during the peak outmigration of juvenile salmon in spring, or in years when zooplankton production is lower than average. Even though biologists studying apex predators are most interested in the abundance and distribution of the forage available during the birds' summer breeding season, the interactions that take place among forage species at other times of the year will influence their summer populations. We have therefore summarized the seasonal diets and diet overlap of these forage species without information on prey selection/preferences or the potential effects of co-occurrence with another species.

Methods - Chapter 1

Data analyzed in this chapter is based on laboratory stomach analysis of forage fish specimens from six, monthly collections in 1994, summer and autumn collections in 1995, and a summer collection in 1996. Field methods are described above in the overall methods for the final report. Fish were identified in the field and preserved in 10% formalin solution; identifications were checked according to a variety of standard keys when fish were measured and weighed in the lab. After stomach analysis in the laboratory, diet composition was computed as percent biomass, percent numbers and percent frequency of occurrence of major prey categories for each forage species in each month. Diet overlap between species pairs was computed for each month in 1994 as the Percent Similarity Index (PSI) of Schoener (1970; Krebs, 1989):

$$PSI_{jk} = \sum \min(p_{ij}, p_{ik}) = 1 - 0.5 * (\sum |p_{ij} - p_{ik}|)$$

where p is the pooled biomass proportion of the i^{th} prey taxon in n taxonomic categories consumed by fish species j and k .

Results - Chapter 1

Fish Size

Stomach analysis was performed on a total of 5110 forage fish specimens representing 14 species in nine sampling periods spanning the three years from 1994-1996 (Table 1). June represented the most intense effort, with up to 496 per species (herring) and a total of 1673 specimens examined. Mean size per species ranged from a low of 31 mm FL for Pacific cod in May, 1994 to a high of 163 mm FL for Pacific tomcod in July, 1995, thus spanning individuals from age-0 to at least age-2. None were noted as gravid or otherwise sexually mature. Seasonal size trends varied among the forage species. Between spring and autumn, 1994, mean sizes of five of the eight forage species consistently caught increased by more than a factor of two (Table 1). They included the gadids and salmonids. Other species either showed inconsistencies in growth across months or were not examined in multiple months.

All three gadids were similar in size and had similar trends of size increase across months of 1994: Pacific cod mean size increased from 31 to 92 mm FL (May-September); Pacific tomcod increased from 47 to 100 mm FL (June-September); and walleye pollock mean size increased from 42 to 107 mm FL (June-November). These fish were principally age-0 (Smith, 1981;

Walters, 1984; Lee, 1985). In July and October, 1995, we also examined small sets of age-1 or age-2, trawl-caught gadids, including tomcod 163 mm mean FL and pollock up to approximately 200 mm FL. Adult Pacific tomcod are the smallest of these gadids, reaching approximately 30 cm length compared to approximately 90-100 cm length for Pacific cod and walleye pollock (Hart, 1983).

Juveniles of two salmonid species also had similar sizes and trends of increase. Mean size of both pink and chum salmon increased from less than 50 mm FL in May to more than 130 mm FL by September, 1994. The salmonids thus tended to be larger in size in a given month than the gadids. The large mean size of chum salmon compared to pink salmon juveniles in July is based on only six specimens (Table 1). The juvenile sockeye salmon examined from June were approximately twice the length of the pink and chum salmon juveniles (104 mm FL) in that month. The pink and chum salmon were YOY fish, while the sockeye salmon could have been age-0 or age-1, since sockeye juveniles can spend a winter in fresh water or go to salt water in their first year of life (Groot and Margolis, 1991). As adults, pink salmon reach a size of approximately 50-60 cm, while chum salmon are larger, up to approximately 80 cm, and sockeye salmon are generally in between these size ranges (Groot and Margolis, 1991).

The mean sizes of three forage species, Pacific herring, capelin and Pacific sandlance, did not increase steadily over the spring-autumn time period in 1994. Pacific herring mean size remained between 123-133 mm FL in the six months between May-November; capelin decreased from 116 mm FL in May to 89 mm mean FL in July; and Pacific sandlance mean size increased from 94 mm FL in May to 127 mm mean FL in June and July, then decreased to 88 mm FL in September. The herring and sandlance were probably age-0 to age-2 (Stokesbury et al, 1998; Dick and Warner, 1982). As adults, herring can reach 38 cm in length and sandlance can reach 26 cm in length. Most capelin were YOY to age-2 pre-spawning adults (Pahlke, 1985; Hatch and Sanger, 1992). Capelin size to 22 cm has been reported from the northern Pacific Ocean (Hart, 1983).

No seasonal size trends were available for five forage species studied: three schooling species (northern smoohtongue, eulachon smelt, threespine stickleback), a nearshore demersal species (Pacific sandfish), and a pelagic species associated with large jellyfish (prowfish). They were all "forage sized," between 80-130 mm mean FL, but tend to be less common in seabird diets. Northern smoohtongue from May, 1994 had mean FL of 80 mm. Smoohtongue mature at 140-170 mm (Hart, 1983), indicating that our samples were juveniles. Eulachon smelt were caught in autumn of 1994 and 1995 at a mean FL of approximately 80 mm. At this size, eulachon in British Columbia were likely age-1 or age-2 (Barraclough, 1964); adults attain lengths of approximately 200 mm (Hart, 1983). Sticklebacks as adults are among the smallest of the species examined, ranging from 25-87 mm (Hart, 1983). Our specimens from May could thus have been adults. Sandfish from July, 1996 were probably age-1 at their 84 mm size (Paul et. al, 1997). Adult sandfish reach approximately 300 mm (Hart, 1983). Prowfish from both July and October, 1996 were 74-92 mm in length. Prowfish to a length of 880 mm have been recorded, but little is known of their life history (Hart, 1983).

Diet Composition

Seasonal prey composition is presented as percent biomass (Table 2; Figure 1), percent number (Table 3), and percent frequency of occurrence (Table 4) of major prey categories. Monthly diet overlap between forage species by prey biomass appears in Table 5. All diet composition values represent monthly pooled samples for each forage species without regard for possible intra-specific differences in diet between size classes, spatial differences in feeding habitat or prey fields available, prey species selected from within categories, forage fish school composition, or diel feeding period. The prey percent biomass measure of diet composition best represents the energy consumed by the fish, but diet composition as percent numbers or frequency of occurrence of prey often present a different picture of common prey items.

Diet composition varied among the forage species and over time. Most were principally planktivorous during the periods sampled. Calanoid copepods were the most consistent zooplankters in the diet. Both large and small calanoid taxa were consumed (total length, TL > 2.5 mm vs. TL < 2.5 mm; weight approximately 30:1). Although large taxa often dominated the calanoid prey biomass, May was the only month in which large calanoids were consumed in greater numerical proportions (Table 3) and more frequently (Table 4) than small calanoids, reflecting the seasonal peak in abundance of *Neocalanus plumchrus/flemingeri* - *Calanus marshallae/pacificus* (hereafter referred to as *Neocalanus/Calanus* spp.; Cooney, 1993). Members of each category of calanoids were difficult to identify when distorted by digestion, and the majority were generalized. However, several genera and species were commonly identified. Among the large calanoid category, these included *C. pacificus*, *C. marshallae*, *N. plumchrus/flemingeri*, *Metridia pacifica* and *M. ochotensis*; less commonly observed species were *Epilabidocera longipedata*, *Eucalanus bungii*, and *Euchaeta elongata*. Small calanoids were principally *Pseudocalanus* spp., with contributions from *Acartia clausi*, *A. longiremis*, and *Centropages abdominalis*, as well as the cyclopoid copepod, *Oithona similis*.

Among the gadids, large calanoids declined in prominence from May to September, 1994. Pacific cod, the only gadid examined from May, consumed almost entirely large calanoids in that month, mostly *Neocalanus* spp., but large calanoids were absent from their diet by September. In June and July, *Neocalanus cristatus* and *N. plumchrus/flemingeri*, *C. marshallae*, *Epilabidocera* and *Metridia* spp. all contributed to cod diet. Other prominent prey of Pacific cod included gammarid amphipods and gastropods (the pteropod, *Limacina helicina*, and unidentified benthic snails) in June and July, and both malacostracans and other epibenthic/epiphytic prey in September. The September epibenthic/epiphytic prey included gammarid and caprellid amphipods, isopods, bivalves, harpacticoid copepods, cumaceans, and polychaetes. For pollock, small calanoids as well as large calanoids contributed substantial prey biomass to the diet, but the biomass proportions of both declined seasonally. Pollock consumed different species of large calanoids each month: in June, *C. pacificus* and *Neocalanus* spp.; in July, *C. pacificus*, *Neocalanus* spp. and *Epilabidocera*; in August, *M. pacifica* and *Euchaeta*; in September, *C. pacificus*; and in October (1995) and November, *M. pacifica*. By late summer, macrozooplankters or fish appeared in pollock diet in larger biomass proportions: hyperiid amphipods in August, fish in September, and euphausiids in November. Pacific tomcod were the least planktivorous of the gadids, with fish prey dominating their diets in three out of four months of 1994. Most prey fish by far were unidentified larvae 10-20 mm in length, but salmonids,

gadids, sandlance and capelin were also observed in stomachs of tomcod and other piscivores. Unlike the other two gadids, Pacific tomcod predation on calanoids was minimal. Like Pacific cod, Pacific tomcod diets commonly included epibenthic/epiphytic organisms, notably gammarids and gastropods, but like pollock, they also ate more pelagic hyperiids. The hyperiids consumed by pollock were *Parathemisto* and other adult species, while those consumed by tomcod were unidentified small juveniles in July and larger specimens later.

The salmonids were consistently piscivorous compared to other forage species excepting Pacific tomcod (Figure 1). Fish were eaten by salmonids in every sampling period. Across the months of 1994, pink salmon diets were approximately one-third fish biomass, one-third calanoid biomass, and one-third other zooplankton biomass (decapods, euphausiids, gastropods, hyperiids). In July, 1996, fish made up approximately 80% of pooled prey biomass of pink salmon. Similarly, chum salmon diets were dominated by fish prey from May-July, and in September, 1994, about 40% of their diverse diet was fish biomass. For sockeye salmon, fish made up over 85% of June prey biomass. Although fish biomass often dominated salmon diets, the frequency of occurrence and percent numbers of fish consumed were usually low (Tables 3 and 4). Fish occurred most frequently in chum salmon diets in May (34%), and least frequently in September (3%); fish occurred in < 12% of pink salmon in all months except September, when 61% of the stomachs contained fish; fish were consumed by approximately 43% of June sockeye specimens (Table 4). Among other prey of salmonids, chum salmon diets never included small calanoid biomass, and large calanoids were minor prey biomass components in diets during all months except August, when they made up approximately 50%. For both pink and chum salmon, large calanoids mainly included *Neocalanus/Calanus* spp. in May; *Epilabidocera* and *Neocalanus* spp. in June; *Epilabidocera*, *Calanus* spp. and *Metridia* spp. in July; *M. pacifica* in August; and in September, *Epilabidocera* for pink salmon and *Euchaeta* for chum salmon.

Pacific herring, capelin and sandlance were planktivorous, the most prominent taxa in their diets usually being calanoid copepods. Fish were rarely important components of these three species' diets and did not contribute to their diets in the same months. For herring, large calanoids remained prominent in the diets from May throughout the summer, with no obvious decline in utilization until autumn. The succession of identified large calanoids by month for herring was, in May and June, *Neocalanus* spp./*C. marshallae*; in July, *Neocalanus/Calanus* spp. and *Epilabidocera*; in August and September, the last three genera and *M. pacifica*; in October, 1995, *M. pacifica*, and in July, 1996 *Metridia* spp. and *Epilabidocera*. Sandlance diet was clearly dominated by calanoid biomass except in June. Large calanoids were most prominent in May, with *Neocalanus* spp., *N. cristatus*, *Metridia* spp., and *C. marshallae* all appearing in sandlance diet. For capelin, large calanoids formed the largest proportion of prey biomass later than for sandlance, in June. Large calanoids in capelin diet included *Neocalanus/Calanus* spp. in May and June, but *Metridia* was prominent in July. Other prey in herring, sandlance and capelin diets varied seasonally. Fish contributed to herring prey biomass only in July (~20%), to capelin prey biomass in May (~60%) and June (~25%), and to sandlance prey biomass in June (~80%). Unidentified malacostraca were prominent in spring diets of herring, while hyperiids, euphausiids and larvaceans became more prominent in late summer-autumn. Capelin tended to consume more of the larger prey taxa earlier in the year than herring. Hyperiids, fish, and euphausiids were large components of prey biomass for capelin in May, June, and July, 1994 compared to later for herring. Euphausiid were also dominant in October, 1995. For sandlance, other taxa besides

calanoids occasionally contributed to prey biomass: fish in June, larvaceans and invertebrate eggs in July, and malacostracans in September. Capelin had higher rates of empty stomachs than herring and sandlance. In autumn, herring, capelin and eulachon had the greatest proportions of empty stomachs observed for all species and all time periods (Table 1).

Seasonal diet trends could not be evaluated for five forage fish species that were examined from only one or two months. The diets of these species are of interest because they are sometimes abundant in the same areas as more commonly-eaten forage species and may therefore compete with them. The diet of northern smoothtongue in May, 1994 was composed of 45% large calanoids (Figure 1, Table 2), predominantly *Metridia ochotensis*. Other prominent taxa included fish, euphausiids, hyperiids and malacostracans. However, 51% of smoothtongue stomachs were empty (Table 1). Sticklebacks consumed nearly half their prey biomass from large calanoids and 40% from fish in May. In autumn of 1994 and 1995, eulachon stomachs contained euphausiids and unidentified malacostracans, but 55-80% of stomachs were empty. Sandfish collected in July, 1996 were piscivorous, with fish occurring in 100% of stomachs (Table 4) and as 97% of prey biomass (Figure 1; Table 2). Small calanoids, decapods and gammarid amphipods occurred frequently and in large numerical proportions, but contributed minor proportions to prey biomass of sandfish. Prowfish prey biomass in July and October, 1995 was more than 80% hyperiid amphipods, principally *Hyperia*. Prowfish also consumed small biomass proportions of larvaceans, small calanoids and pelagic gastropods (the pteropod, *Limacina helicina*). Gut contents of prowfish also had unquantifiable, gelatinous material that appeared to be from “tentacle-nibbling” the jellyfish.

Diet Overlap

Diet overlap between species was most common in June, 1994, when nine species were examined. Diets of one-third of all species pairs (12/36) overlapped significantly (> 60% PSI), with many values in excess of 75%. The degree of similarity varied mostly with the proportion of large calanoids and fish in the diets, and sometimes the proportion of small calanoids. Sandlance and capelin diets each overlapped with three different species, but not with each other. Capelin diet overlapped with Pacific cod, walleye pollock and Pacific herring diets (60-84%). Sandlance diet overlapped with Pacific tomcod, and sockeye and chum salmon diets (76-87%). Pacific cod and Pacific tomcod also overlapped with three different species each. Pacific cod overlapped with herring, pollock and capelin 60-66%, while tomcod overlapped with sockeye, chum and sandlance 80-87%. Pollock and chum salmon diets each overlapped with three species, but not with each other. Pollock diet overlapped with Pacific cod and herring by 65-66% and with capelin diet by 84%. Chum salmon diet overlapped with Pacific tomcod, sockeye salmon, and sandlance diets by 84-85%.

Few other patterns in diet overlap were observed. In May, threespine stickleback diet overlapped with three species (pink salmon, northern smoothtongue, and capelin) by 62-73%. Significant diet overlap was scattered among other species pairs in May: pink salmon overlapped with smoothtongue (69%), sandlance with Pacific cod (84%), and chum salmon with capelin (75%). In July, sandlance diet overlapped with pollock's (81%), Pacific tomcod overlapped with Pacific cod, pink salmon and herring (61-68%), and pink salmon overlapped with Pacific cod and Pacific tomcod (60-65%). Diet overlap between species pairs was rarely consistent across

months. The most consistent species pairs for which we have data are pollock and herring, whose diets overlapped significantly in June and November, 1994 and in July and October, 1995. Pacific tomcod and pink salmon diets overlapped in July and August, 1994. Sandlance and herring diets overlapped significantly in September 1994 and July, 1995, but not in July, 1996. Capelin diet overlapped with both sandlance and herring in July, 1995.

Interannual Diet Patterns

Some species showed interannual consistencies in diet while others showed interannual differences. Interannual patterns of consistent diet composition were noted for pollock and sandlance in July, 1994-1996, when small calanoids predominated in their diets and large calanoids made up smaller biomass proportions. Larvaceans (a small prey) were numerically prominent and contributed notable biomass to sandlance diet in July of all three years. Pollock diets were also very similar in November, 1994 and October, 1995. In contrast, interannual differences between July diets were observed for Pacific tomcod, Pacific herring, capelin, and pink and chum salmon. For tomcod, the prey taxa present in July diets were highly diverse, and July, 1996 was the only period in which fish were not present in the diet. For herring, calanoids were the predominant taxon in July of each year, but diets differed in the proportions of large and small calanoids consumed, and in the appearance of decapods, fish or gastropods in the diet. Similarly, in October-November of the two years, large calanoids and euphausiids were each consumed but the proportions differed. Capelin diets differed radically between the years. Large prey were consumed in July, 1994 (large calanoids and euphausiids) and small prey were consumed in July, 1995 (small calanoids). Pink salmon were much more piscivorous in July, 1996 than in 1994 or 1995; in the first two years, diets were very similar based on large calanoids, fish and gastropods. On-the-other-hand, chum salmon were least piscivorous in 1996. Their diets included more prey biomass from hyperiids and either chaetognaths or decapods in July of 1995 and 1996 compared to mostly fish in July, 1994.

Discussion - Chapter 1

Collectively, the 1994-1996 Forage Fish Diet Overlap investigations confirm that the 14 forage species examined are largely planktivorous from May-November in their first two-three years of life. Common prey items included large and small calanoids, pteropod gastropods, hyperiid amphipods, euphausiid larvae in summer and older stages in autumn, and larvaceans. Prey composition changed seasonally for the eight species examined monthly from April-September. The biomass composition of large calanoids in the diet generally declined after spring, prey became more diverse, and macrozooplankters became common in diets.

Seasonal size trends are important to note because fish body size is often correlated with diet composition. Just as trends of increasing mean size across several months reflect growth, lack of growth can indicate the influx (recruitment) of YOY fish or an inshore spawning migration of adults. In some months, catches of the three species with little apparent growth over the months (herring, capelin and sandlance) include bi-modal size distributions representing multiple age classes (data on file). This is suggested by the wide size range and by standard deviations up to approximately 20% of the mean. Monthly changes in mean size of the species examined are

influenced by factors such as differences in the onset and duration of spawning time and the appearance of the larvae, ontogenetic changes in spatial distribution, and size selectivity of the gear. Some of these life history traits, such as spawning, are controlled by temperature. Northern smoohtongue spawning, for example, begins in mid-autumn and ends in spring (Sobolevsky and Sokolovskaya, 1996), while herring spawn in mid-spring (Brown et al, 1996) and capelin in late spring and summer (Pahlke, 1985). A wide size range of larvae and juveniles of species with protracted spawning periods could occur in an area at the same time. The co-occurrence of species or certain size groups of species with another may also be influenced by growth rates. Walters (1984) found that of YOY pollock, cod and tomcod in Port Townsend, Washington, the cod grew the fastest and were the first to begin leaving the nearshore nursery areas shared in summer; pollock left later, followed by tomcod late in the year (Walters, 1984). Size-diet trends among these forage species will be investigated in future.

Forage fish diet composition in PWS was similar to that reported from studies done elsewhere. Juvenile pollock in the Gulf of Alaska are commonly reported to feed on small calanoids in summer and euphausiids in autumn, with size related shifts in prey (e.g., Kamba, 1977; Krieger, 1985; Merati and Brodeur, 1996). Although studies on pollock have increased in recent years, little has been published on the morphologically similar, but not commercially important, juvenile Pacific cod and tomcod. A study on the Olympic Peninsula, Washington examined all threegadid species from May -September (Walters, 1984). Juvenile Pacific cod fed mainly on small calanoids, harpacticoids, mysids and gammarid amphipods. Calanoids became less important as mysids and gammarids became more important in larger juveniles' diets, and shrimp and polychaetes appeared in the largest individuals. Growing Pacific cod thus exhibited an increasingly benthic feeding mode as well as prey size increase. In the same study, pollock and tomcod fed on the same prey categories as cod, but pollock, and tomcod to a lesser degree, continued to prey on calanoid copepods longer than cod. Unlike in our study, euphausiids were not important in these species diets (Walters, 1984). In Kamchatkan waters, cod up to 200 mm principally consumed amphipods, mysids, and euphausiids (77-91% biomass) and some fish (Tokranov and Vinnikov, 1991). The diet was more similar to cod in our study. In the eastern Bering Sea, cod and pollock up to 75 mm TL were studied in summer (Lee, 1985). Prey composition was related to differences in prey availability as well as to morphological differences in the fish (gill rakers) that influenced prey size selection. Pollock were adapted to feeding efficiently on small organisms; they had greater numbers of gill rakers closely-spaced compared to fewer rakers widely-spaced in Pacific cod (Lee, 1985). Diet overlap was high for individuals < 40 mm TL. At approximately that size, cod diet changed abruptly to larger food items, including fish prey; at the same time, the spacing between gill rakers in cod increased with growth, again indicating an adaptation to predation on macrozooplankton and piscivory (Lee, 1985; Tokranov and Vinnikov, 1991). We found tomcod to be generalists, feeding on benthic and pelagic prey--even the large copepods they ate ranged from surface swarming *Epilabidocera* to the strong vertical migrators, *Metridia* spp. Pollock, on the other hand, had a narrower prey suite that was restricted to smaller items for a longer period. The details of such prey size preferences need further study.

Copepods are commonly reported to be the main food of other young fish. For Pacific sandlance, small calanoids and other small taxa are prevalent; epibenthic taxa can be important in both fall and winter and euphausiids can be important in winter (Field, 1988; LeBrasseur et al,

1969; Craig, 1987). Few studies have compared Pacific sandlance feeding to other forage species (Simenstad et al., 1979; McGurk et al, 1992). In a study of neritic fish assemblages in Puget Sound, juvenile Pacific herring, Pacific Sandlance, and pink salmon were grouped into one functional feeding group, pelagic planktivores (Simenstad et al., 1979). Sandlance and herring were defined as obligate, while pink salmon were considered facultative planktivores. The diets of all were dominated by calanoid copepods, although overlap was not reported (Simenstad et. al, 1979). Further north, in a southeast Alaska bay, juvenile herring and capelin diets overlapped in spring when both fed in the water column (Coyle and Paul, 1992), then diverged when the water column stratified; herring then fed at the surface, while capelin continued to feed in the water column. In April, large calanoids were the most important prey of capelin, and were less important in herring diet. In May and June, small calanoids were important in both species diets, and herring switched from barnacle nauplii to barnacle cyprids. Juvenile sockeye salmon in the same study foraged near the surface in June, mainly on oikopleurans and barnacle cyprids, and their diets overlapped substantially with juvenile herring diet at that time (Coyle and Paul, 1992). In another study of herring and capelin in early summer in the Barents Sea, prey biomass was comprised mainly of calanoids, oikopleurans and larval euphausiids, with diet overlap highest among specimens 80-135 mm in length. Diet shifted ontogenetically and similarly, with consumption of calanoids declining and consumption of euphausiids increasing with size (Huse and Toresen, 1996). These studies and ours show that, like the gadids, the trophic relationships of these co-occurring species change over time and with size. Huse and Toresen (1996) concluded that herring and capelin could compete for food when planktivores were abundant or prey resources were limited.

Pink and chum salmon are typically planktivorous during their early marine period. These two species often very similar diets (e.g., Murphy et al, 1988; Landingham et al, 1998). However, juvenile chum salmon commonly feed more on epibenthos than do pink salmon (e.g., Murphy et al, 1988), and are size selective predators (Groot and Margolis, 1991). Both species were planktivorous in PWS, but pink salmon preyed more on small calanoids and chum salmon preyed more on large calanoids (Sturdevant et al, 1996). Their diets also varied with habitat, both species consuming more epibenthic prey in low-gradient habitats than in medium- and steep-gradient habitats. Both pink and chum salmon fry feed heavily on epibenthic prey in some regions (Groot and Margolis, 1991). Sockeye salmon juveniles typically eat macrozooplankton and fish, and calanoids are not important prey (Groot and Margolis, 1991). However, Landingham et al (1998) found interannual changes in the July-August diet for all three species, from crustaceans to fish, and their diets overlapped significantly. In our study, chum salmon were more piscivorous at a smaller size than pink salmon (Figure 1).

In a separate analysis of the August-September, 1994 data, Willette et al. (1995; 1997), used principal components analysis (PCA) and cluster analysis to identify similar diet composition between juvenile pink and chum salmon, between juvenile Pacific herring and walleye pollock, and between capelin and sandlance. Higher diet overlap was identified between the first two species pairs than between other species pairs, and between sympatric species pairs than for allopatric species pairs. Small calanoid copepods in general (and *Pseudocalanus* spp. specifically) and larval fish prey were partitioned (PCA). Juvenile herring and pollock consumed more calanoid biomass than juvenile salmon, while juvenile salmon consumed more larval fish biomass. Juvenile chum salmon also preferred gelatinous prey, such as ctenophores, cnidaria, and larvaceans. Diet

composition and overlap changed significantly over a diel period (Willette et al., 1995; 1997).

Smoothtongue diet in our study was similar to their diets in other parts of the north Pacific. In the Strait of Georgia in April, northern smoothtongue stomachs contained euphausiids, copepods, barnacle larvae and fish eggs (Hart, 1980). In the Bering Sea in June, large calanoids (*Metridia pacifica*) comprised more than 50% and oikopleurans comprised 12% of prey biomass in northern smoothtongue diet (Gorbatenko and Il'inskii, 1991). Diets differed between summer and autumn (Balanov et al, 1995b). The dominant food organisms by weight included euphausiids and two large calanoid species, (*Neo*)*Calanus cristatus* and *Eucalanus bungii*, in summer and 90% euphausiids in autumn. In another Bering Sea study in autumn, euphausiids, jellyfish and *Oikopleura labradoriensis* were the predominant prey (Balanov et al, 1995a), while in eastern Kamchatka in early winter, cnidarians and ctenophores contributed more than 65% biomass of diet in northern smoothtongue. Smoothtongue is a mesopelagic species that performs a strong vertical migration. Smoothtongue predation on the large calanoid, *Metridia ochotensis*, in our study can be explained by the overlap in vertical distribution of these two migrators. Although significant diet overlap was observed between smoothtongue and pink salmon, the large calanoids on which it was based were mostly different species, since pink salmon mainly ate *Neocalanus*. These diet differences indicate that they fed at different depths in the water column. Sobolevskii and Senchenko (1996) found no more than 45% overlap between the diets of northern smoothtongue and either pink or chum salmon or walleye pollock. However, the autumn diet change reported by Balanov et al (1995), along with our results, suggest that smoothtongue diet could overlap with pollock, herring and capelin then. More information on this species is needed to clarify trophic relationships.

Threespine sticklebacks are a very generally distributed fish found in both fresh and saltwater. Their diet of large calanoids and fish overlaps with nearly all the other forage species based on one of the two categories. Other studies showed that stickleback diet consists mainly of copepods in spring and autumn, but a wide variety of small, marine and brackish water crustaceans and young fish are also prey (Hart, 1983). They have been shown to compete with sockeye salmon in freshwater (Groot and Margolis, 1991). Diet overlap with small individuals in early spring seems likely, but we have no data to support this.

Eulachon are potential competitors of capelin, herring, smoothtongue, and pollock for euphausiid prey in autumn. In other studies, juvenile and adult eulachon also ate euphausiids and copepods (Hart, 1983). Juvenile eulachon from the echo scattering layers in the coastal waters of British Columbia had guts full of the euphausiids abundant in these layers (Barraclough, 1964). However, the high frequency of empty stomach that we observed suggests that feeding is reduced in autumn for both capelin and eulachon (Winters, 1970). Eulachon is another species for which additional studies are required to improve our understanding of trophic interactions.

Sandfish are a little-known, burrowing, intertidal species often caught in small numbers in beach seines. Their diet was very similar to pink salmon in July, 1996 (Figure 1). Although young sandfish do school with pink salmon (Bailey et al, 1983), we could not determine whether the individuals we caught were in the water column or were buried in the sandy gravel. They were smaller than mean size of salmonids, slightly larger than mean size of herring and tomcod, and similar to mean size of sandlance. However, at a mean length of 85 mm, they were larger than the

fish they directly co-occurred with on western Bligh Island, sandlance (72 mm) and herring (48 mm). In another study, young sandfish (33-42 mm SL) were sympatric with pink salmon (40-59 mm SL) from Southeast Alaska in June. These sandfish were completely planktivorous, and diet overlap with the pink salmon was nearly 70% by number (Bailey et al, 1983). Shared prey included euphausiid larvae, calanoid and harpacticoid copepods, and larvaceans; fish did not appear in either species' diet (Bailey et al, 1983). By contrast, Paul et al (1997) found that sandfish < 100 mm (62-99 mm FL) consumed shrimp, euphausiids and decapod larvae most often, with sandlance occurring in approximately 9% of the stomachs; sandfish > 100 mm (115-303 mm FL) were primarily piscivorous on sandlance and other fish. An examination of numerical or frequency composition of prey for these species in our study gave similar results. In July, 1996, sandfish diet was 75% small calanoids by number (Table 3) but gammarids occurred most frequently after fish prey (46%; Table 4); pink salmon diet was 88% larvaceans by number, with the frequency of gastropods, small calanoids and larvaceans between 41-83%, respectively. The highly similar diets of sandfish and pink salmon that we have shown were therefore not based on the most prevalent prey taxa. All three of these studies point to the high potential for competition between juvenile pink and chum salmon and sandfish, because of their similar habitat and diets during the salmonid's early marine period, particularly at times or in areas where fish prey are not available. What is not obvious is the numerical diet overlap between the sandfish, sandlance and herring that actually co-occurred. All three of these species consumed more than 75% small calanoids by number (Table 3), and although the sandlance and herring diets were also dominated by small calanoid biomass (\$ 61%), sandfish diet biomass was primarily fish present as # 1% numbers.

The presence of gelatinous material and *Hyperia medusarum* in prowfish stomachs suggest that prowfish take advantage of the parasitoid relationship between jellyfish and some hyperiids (Brusca, 1981) while obtaining shelter from the jellyfish. Most other forage species that sometimes consume hyperiids are not associated with jellyfish and are therefore unlikely to compete with prowfish. Pollock associate loosely with jellyfish for shelter (e.g., Brodeur, 1998), but salmonids are not associated with jellyfish. Prowfish diet did not overlap significantly with other July species, although pink and chum salmon and pollock also ate hyperiids. In fact, the hyperiid fauna were partitioned, since pink and chum salmon principally consumed *Themisto pacifica* and *T. libellula*. Hyperiids were < 10% of prey biomass pollock diets. Of interest, these other forage species also eat gelatinous prey at times. Chum salmon prey on the salps with which *T. pacifica* is associated (Brusca, 1981). Juvenile chum consumed up to 6% of prey biomass from such gelatinous taxa in late summer, 1994 (Table 1; see also Willette et al, 1995; *ibid*, 1997). We observed up to 4% prey biomass from cnidarian/ctenophore tissue in pollock guts (November, 1994).

Planktivorous forage species shifted diets seasonally from predominantly calanoid biomass to predominantly macrozooplankton biomass. The shift was more gradual for species such as herring and pollock than for some others. However, large and small calanoids were consumed throughout the spring, summer and autumn, and a variety of different macrozooplankters were consumed summer through autumn. Forage species preyed on a succession of large calanoids as they became available, yet some partitioning among the species occurred. Facultative predation on *Neocalanus* spp. was observed when this genus was abundant in May and June (e.g., Cooney, 1993). Chum salmon and capelin were the only fish species that did not consume substantial large

calanoid biomass; both were largely piscivorous in May. When large calanoids were the common prey category between species with high diet overlap, the actual degree of diet overlap could be much lower than we estimated from pooled taxa. For example, in May, more than 30% of smoohtongue diet biomass was a large calanoid species not consumed by other fish (*Metridia ochotensis*), thus reducing the amount of actual overlap with pink salmon or stickleback. Also unlike the other species, sandlance consumed a diverse array of large calanoid species in addition to *Neocalanus* in that month. The calorie-dense large calanoids were less prominent in forage fish diets in summer when the peak bloom of *Neocalanus* spp. had passed but fish were larger. Other large calanoid species were more common than *Neocalanus* spp. in summer and autumn, especially *M. pacifica* and *Calanus* spp., but generally did not contribute as much prey biomass as did *Neocalanus* spp. in the spring. In June, sandlance and the salmonids consumed only small proportions of large calanoids. In July, different fish species tended to share different large calanoid resources, ie., prey species overlap was limited to a few fish species. In July, 1994, for example, herring mainly consumed *Neocalanus/Calanus*, while capelin mainly consumed *Metridia*, but pink and chum salmon preyed on *Epilabidocera*, *Calanus* spp. and *Metridia* spp. These differences could represent stratification of feeding by depth in the water column (Coyle et al, 1992) as well as oceanographic influences on copepod distribution and availability to predators. As mentioned above, however, fish size and ontogenetic diet shifts are also important to consider. The interannual consistency of sandlance and pollock diets in July compared to the interannual variation of herring and capelin diet suggests that for some species, prey composition was influenced by size differences as well as species interactions. Herring mean size was smaller in successive months of July, 1994-96 (130 mm-75 mm FL), yet much of their prey biomass was consistently calanoids. Capelin were age-1 in July, 1994 compared to age-0 in July, 1995, and the interannual differences in diet composition reflect ontogenetic shifts in prey size selection (Figure 1). However, sandlance mean size indicates fish were age-2 in 1994 compared to age-1 in 1995 and 1996, yet diet was quite constant in the three July months. Thus, species must be considered individually in the context of their life histories.

Most forage species were planktivorous at the times and in the size ranges we sampled. The least planktivorous species were the tomcod, salmonids and sandfish. However, both opportunistic piscivory and size-related shifts to piscivory were observed among the planktivores. Opportunistic piscivory was exhibited by some species that did not consume fish in the summer but did prey on fish larvae in spring, such as sandlance in June and capelin in May. Even though it was earlier in the year, the mean size of these fish was larger at the time they ate substantial biomass proportions of fish compared to when they did not, again suggesting a bi-modal size in the specimens examined. Size-related shifts to piscivory were clearly observed for species such as pollock and herring when they were beyond the general size maximum of seabird prey, approximately 150 mm FL (Sturdevant, 1995; Sturdevant and Willette, 1995; Chapter 1, this report). A trend for partitioning by prey size and type is also suggested in Figure 1 for herring, capelin and sandlance. Overall, sandlance consumed smaller prey more often than the other two species, and capelin tended to consume larger prey earlier in the year than herring. Unlike the gadids, mean size of these species did not obviously increase over time and diet trends for these species also suggest that multi-modal size classes were examined. Spring herring, capelin and sandlance diets included relatively large biomass and frequency of fish that are not observed in later months (Figure 1, Tables 2-4).

Prey fish in the size range that subadult forage fish can consume include the larvae and fry of numerous taxa. Fish larvae are most abundant in the ichthyoplankton in spring (May/June) in the upper 50 m (Haldorsen et al, 1993; Norcross and Frandsen, 1996), but in PWS, oceanographic features also influence the distribution, density and species composition of ichthyoplankton from April to October (Norcross and Frandsen, 1996). Spatial differences in the density/availability of fish larvae may explain the patchiness of piscivory among large fish specimens at some stations compared to others (e.g., pink salmon in July, 1996). Fish grow faster when piscivorous than when zooplanktivorous (Juanes and Conover, 1994; Mittelbach and Persson, 1998), but despite the ontogenetic increase in mean prey size of piscivores, many species continue to select small prey (Juanes, 1994). We observed this in the salmonids and tomcod, for example. The onset of piscivory in fish is generally believed to occur earlier and at smaller sizes in species that are born larger and have bigger gapes, and different piscivores of similar size consume similar sized prey (Mittelbach and Persson, 1998).

Few investigations of carrying capacity have included the consumptions of as many fish species as we have studied. Since population estimates of most forage and other fish species for PWS are not available, it is difficult to estimate the impact of their feeding on one another in the sound. The food requirements of numerous species have not been well-documented, not only in terms of prey composition but in terms of daily ration. The carrying capacity of PWS for juvenile Pacific salmon has been estimated, however. Cooney (1993) estimated that juvenile salmon (mostly pinks) with growth rates averaging 3-4% of body weight daily use up to 3.2% of the total 'herbivore' production and up to 10.0% of the annual macrozooplankton production in the region, when mortality is accounted for. Since the planktivorous and piscivorous feeding of juvenile salmon overlaps with a number of other forage species, some of this mortality will be impacted by trophic interactions among the fish, both through food competition and predation. Although most of the other forage populations are likely not as large as the salmonids', more than half of which comes from hatchery production (Cooney, 1993), if each of the 10 or so other species included in this study consumes just half the maximum estimate for juvenile salmon, then approximately 1/4 of the total herbivore production and 3/4 of the macrozooplankton production would be consumed. As noted above, some of these species, including the salmonids, also utilize some ichthyoplankton prey resources during their period of residency. In addition, some forage species live longer than pink salmon, but mature at smaller size, and, unlike the salmon, remain in PWS to complete their life history. In other areas of the northwestern Pacific, researchers have provided evidence that juvenile salmon crop the epibenthic and neritic prey resources they utilize; declining foraging success and the availability of preferred prey organisms related directly to migration rates of juvenile salmon out of estuarine and nearshore areas (Simenstad and Salo, 1982) and distribution and residency were food-limited at certain times (Healey, 1982). An impact of salmonid feeding was also documented in the Gulf of Alaska, where they continued to depress macrozooplankton stocks (Shiomoto et al, 1997), but limits to the ocean's carrying capacity continue to be debated (Heard, 1998). In all of these areas where salmon impact their feeding environments, forage species and other residents will also experience the decline in prey resources, but how the inevitable trophic interactions affect forage fish availability to seabirds has not been studied. We need long term studies of fish feeding and both mesozooplankton and macrozooplankton trends.

Jellyfish competition with forage fish is a new aspect of the PWS ecosystem being investigated (Purcell et al, 1999). The summer diets of four large species of pelagic cnidarians

(*Aurelia*, *Cyanea* and *Aequorea*) and a ctenophore (*Pleurobrachia*) were compared to those of juvenile walleye pollock, sandlance, herring and pink salmon. Collectively, both predator groups principally ate small calanoid copepods and larvaceans. Other jellies that occur in the nearshore feeding zones occupied by small forage species, such as the small medusa, *Irene* spp., probably also consume small zooplankters. The similarity between diets of these jellyfish and forage fish suggest the two groups may compete for food resources in areas or times of low plankton abundance. Other recent studies suggest that forage fish populations may also compete with marine organisms besides jellyfish for zooplankton, including chaetognaths (Baier and Purcell, 1997), euphausiids (Atkinson and Cripps, 1999), aquatic insects (Herwig and Schindler, 1996), and hydroids (Madin et al., 1999). Further multi-species studies which examine competitive interactions of planktivores at several trophic levels are needed to examine the carrying capacity of PWS for forage fishes.

Diet overlap changed between species pairs each month and sometimes reflected growth patterns. Lee (1985) concluded that competition between co-occurring cod and pollock would vary according to their size combinations, and would be greatest when individuals of both species were < 40 mm. In our study, the gadids were in this size range in May and June (Table 1), but no pollock were examined from May. Indeed, the only time we observed significant diet overlap (66%) between cod and pollock was in June, when they were smallest. Then in July, cod and tomcod diet overlapped significantly (61%), reflecting cod's change to larger prey and the onset of piscivory at larger size (Figure 1). Pollock switched to large prey later than cod and tomcod. Pollock began to eat macrozooplankton at 73 mm in length and fish at 92 in mm length, compared to the 55 mm length of the other gadids. Consequently, pollock and tomcod diets overlapped in September (75%). Pollock are significant piscivores and cannibals as adults (Dwyer et al, 1987).

June appeared to be a time when food webs were most complex. June was also the month when the quality of capelin for piscivorous seabirds was highest (Roby et al, 1998). Numerous factors can influence fish diets. For example, the prey suite available to fish in an area may change with time or may vary in different habitats; growth to larger body size may be accompanied by increased swimming speed and mouth gape, which facilitate predation on different taxa; increasing energy requirements may be more efficiently met by consuming larger items if the costs of consuming them are not too great; and forage fish interactions with other species may prompt shifts in prey consumption to avoid potential competition. Investigation of these possibilities was beyond the scope of this chapter. Calanoids, fish and macrozooplankton were used to varying degrees by all forage fish species, but as prey composition changed monthly and with size, diets of different species pairs overlapped. Herring and pollock were the most consistent pair with overlapping diets. Chapters 2 and 3 discuss the importance of considering the frequency and duration of species co-occurrence to evaluate the importance of diet similarity.

The influences of different diets of forage species on their nutritional quality and growth are an area of study needing more intensive study. Energy assimilated from the diet can be allocated for lipid storage, such as for gamete production, or for somatic growth of fish. The diets of forage fish could influence both their nutritional quality and, through size of fish, their effective availability as forage for seabirds. Payne et al's (1997) studies of the proximate composition of 14 forage species in the northeastern Pacific showed large differences between species. The smelts/osmerids had the highest oil content, sandfish/pricklebacks/sandlance were

intermediate in oil content, and pollock/herring/prowfish were among those species with the lowest oil content. The generally high lipid content of pelagic species maturing at small size (herring, sandlance and capelin) nonetheless varied intraspecifically with age, sex and collection site (Anthony and Roby, 1997; Roby et al, 1998). Roby et al. (1999) found both interspecific and intraspecific differences in lipid content of seabird prey dry mass (2-61%), resulting in a fivefold difference in energy density. Seabird prey choice could thus reflect huge differences in forage fish quality and influence reproductive parameters.

Heintz et. al (1999) were able to detect fine-scale spatial differences in the triglyceride (TAG) content of sandlance collected from adjacent bays in southwestern PWS, yet sympatric herring and sandlance both had greater amounts of TAG than allopatric herring and sandlance. This result suggests that prey availability affects nutritional content more than trophic interactions between planktivores do. Yet our observations of subtle shifts in prey composition, and especially, the declines in food quantity consumed by sympatric forage species compared to allopatric forage species (Chapter 3) suggest that competition is a mechanism by which diet can influence nutritional content. Studies on the chemical composition of zooplankton showed that copepods contain the largest fraction of lipid, while protein content varied relatively little between copepods, pteropods, polychaetes, amphipods, cnidarians and ctenophores (Ikeda, 1972; Lee, 1974). Protein was highest and lipid was among the lowest values for euphausiids and chaetognaths (Ikeda, 1972). Copepods stored lipid, while other zooplankters (ostracods, pteropods, euphausiids amphipods and decapods) stored triglycerides (Lee, 1974) and oikopleurans did not store lipid (Deibel et al, 1992). Lipid content in zooplankters, as in fish, is related to ontogenetic stage (Deibel et al, 1992). In addition to their nutritional content, the relative abundances of preferred zooplankters vary. In particular, long-term studies of zooplankton production in PWS have revealed that the standing stock of large calanoids (*Calanus/Neocalanus*) and small calanoids (*Pseudocalanus*) not only varies interannually but varies with regard to which category predominates (Cooney et al, 1994). Other taxa are no doubt similarly variable. Since small calanoids are the predominant taxon available in summer and autumn zooplankton (see Chapters 2 and 3), non-selective feeding at high rates on small calanoids could favor small forage fish with high-lipid requirements without high energy expenditure. Even if other taxa provide more calories in larger packages, feeding on small calanoids for lipid combined with other abundant zooplankters, such as gastropods, oikopleurans or euphausiids, for other nutrients may supply the most advantageous diet. Similarly, diet may explain monthly variation in lipid content and energy density (Roby et al, 1998), since the proportional biomass of calanoids in the diet of forage species declined seasonally and other prey varied monthly. Something other than diet must explain the very different proximate compositions of planktivores such as herring and pollock that have similar diets at similar size/age.

We do not have lipid content or energy density values for the forage specimens whose diets we examined. However, lipid content was generally ranked highest for adult eulachon/lanternfish, second for herring, third for sandfish, sandlance and capelin, fourth for prowfish, and fifth for salmonids and gadids (Roby et al, 1998). Young fish generally had lower lipid content than larger/older fish (Roby et al, 1998). Given our diet information and the nutritional profiles noted above, diets of forage species may be adapted to their life history strategies. A diet high in protein, as is supplied by fish prey, allows faster growth (Harris et al, 1986). Faster growth allows young fish a predation refuge from size-selective piscivores that

prey on smaller individuals (Hargreaves and LeBrasseur, 1986). Gadids and salmonids mature at larger size than herring, capelin or sandlance. The salmonids in our study were most piscivorous, with growth advantages that are important for their long migration to the Gulf of Alaska. The other species do not perform such an extensive migration and can afford to remain planktivorous longer, yet the higher lipid content of such a diet may allow earlier maturity. The timing of reproduction may be timed according to forage species seasonal diet shifts and predation on a succession of prey resources. Gamete production requires high energy intake, so fish maturing at small size should do better as planktivores that feed on high lipid plankters such as copepods or maturing macrozooplankton instead of on fish larvae. The late copepodite stages of *Neocalanus* consumed in spring are a prime example. Ontogenetic partitioning of prey resources among forage species may thus be advantageous for both strategies. Selective predation by piscivores on the faster growing, larger forage specimens that prey on fish and larger taxa when younger and smaller, would tend to select for slower growth rates and planktivorous life style forage species.

Other effects on diet and nutrition may be density dependent. For example, in years with high abundances of forage species having inferior nutritional quality, such as 1995 appeared to be for YOY pollock (Haldorsen et al, 1996), competition for similar prey between pollock and nutritionally superior species, such as herring, could influence both the energy content and size of the birds' preferred forage species. Herring energy density differed between 1995 and 1996 (Roby et al, 1998), but our interannual diet data are limited to the months of July and come from different areas of the sound. We observed interannual differences in prey consumed during July by tomcod, pink and chum salmon, and herring, indicating that the lipid and therefore energy content of forage fish could vary between years. However, these species sizes also varied between years. Tomcod were much larger in 1995 than in the other two years, pink salmon were smallest in 1994, chum salmon were largest in 1996, and herring size declined from 1994-1996. Pollock size differed little between July, 1994 and July, 1995. Roby et al. (1998) showed that younger fish generally had lower lipid content. Since fish grow faster on fish prey, the onset of piscivory or switch from predation on mesozooplankton (copepods) to macrozooplankters could also influence forage fish effective availability to seabirds which provision their nestlings with fishes in certain size ranges during the brief summer. The area fished and the gear used also differed between years, so our samples are not equally representative of species' size classes. Our results indicate that planktivory is a factor that can determine the abundance of the preferred forage species of seabirds, but that careful consideration must be given to many factors, including sampling methodology, spatial and temporal distribution, allopatry vs. sympatry, school density, size distribution, and the prey available when evaluating results of diet analyses, and that directed sampling and perhaps manipulative studies are necessary to further elucidate the impacts of these variables.

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Acknowledgments - Chapter 1

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